Epidemiology of Verticillium Wilt of Cotton: A Relationship Between Inoculum Density and Disease Progression

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ABSTRACT

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Inoculum density of *Verticillium dahliae* in field soil in May was related to mid-September incidence of foliar symptoms of Verticillium wilt in cotton over a period of 7 yr within two adjacent fields in California. Disease progress curves for each growing season showed a highly significant straight line relationship with time when high air temperatures did not inhibit disease development. Slope values of the disease progress curves were related to inoculum density of *V. dahliae* at population densities below 40 propagules per gram (p/g) of soil. In weekly samplings throughout the season, percentage of plants with foliar symptoms was always less than the percentage of plants with vascular discoloration. The differences between these two symptoms increased during periods of high air temperatures when further development of foliar symptoms was arrested. Inoculum density of soil sampled in May increased on the average of 13–15 p/g per year in soil continuously cropped to cotton. The naturally occurring pathotypes present in the experimental field sites ranged from nondefoliating to partial defoliating. Approximately 19% of the leaf isolates tested were classified as nondefoliating, 72% as intermediate types, and 9% as defoliating.

Additional key words: *Gossypium hirsutum*, soilborne pathogens.

Verticillium wilt of cotton (*Gossypium hirsutum* L.), which is caused by *Verticillium dahliae* Kleb., can become a major disease problem in soils cropped continuously to cotton (4,8).

This disease is currently managed through the use of tolerant Acala cotton cultivars, crop rotation, and cultural practices; however, highly virulent strains or pathotypes of *V. dahliae* exist in California soils and often cause significant losses in cotton lint yields (24).

Recent work on Verticillium wilt indicates that the percentage of cotton plants with vascular discoloration is closely related to inoculum density (ID) in the soil (2,5); however, the occurrence of foliar symptoms in relation to ID is variable and highly sensitive to environmental conditions (9).

In the present study, variation in the ability of inoculum of different pathotypes to cause disease was minimized by using a single field site for several successive years. Throughout the study, the fungal pathotypes present were mainly nondefoliating. The objectives of this study were to determine the relationship of ID near the time of planting to disease (foliar symptoms) progression and to compare the incidence of vascular discoloration and foliar symptoms throughout the growing season. The results of this study will be used to develop a model of Verticillium wilt of cotton that is linked to models for cotton plant growth and development and for cotton defoliation caused by *Lygus hesperis* 13).

MATERIALS AND METHODS

General description of field area. Field plots (8 × 40 m) were established within a 2.3-ha field located near Five Points, CA. These plots were on a deep deposit of Panoche clay loam in which a high incidence of Verticillium wilt had been observed in previous cotton crops. From 1973–1979 these plots formed the nucleus of several field studies on the control of Verticillium wilt by soil flooding, paddy rice rotation (7,19), or soil heating by solarization (22). These plots, along with those from an adjacent 0.5-ha field, provided areas with varying inoculum densities.

Each year, plots were either planted with Acala SJ-2 cotton; rotated for one season to paddy rice, upland rice, or soil flooding alone; or solarized and planted to cotton the following year. The soil in all plots was sampled in May, within several weeks of planting, to determine the soil population density of *V. dahliae*. If cotton was planted, the incidence of Verticillium wilt based on foliar symptoms was determined weekly from late June to mid-September or in mid-September only. Cotton was grown in rows 1 m apart and thinned to approximately four plants per meter of row. Standard irrigation and cultural practices were followed throughout the growing season. All cotton crops were furrow irrigated except the 1979 crop, which was sprinkler irrigated.

Field experiments, 1977. A subplot 4.1 × 6.1 m, containing approximately 100 plants, was established within each 8 × 40-m field plot. Soil samples and disease ratings were taken within these areas. Disease incidence (DI), indicated by the presence of two or more leaves with foliar symptoms of Verticillium wilt, was monitored either weekly from late June until mid-September or in mid-September only.

Cotton was planted in a second field (0.5 ha) adjacent to the main field. Six 3.1-m sections of row were marked off within the field. Consecutive plants in each of these rows were examined weekly for foliar symptoms of Verticillium wilt from first square (flower bud) formation until mid-September.

Field experiments, 1978 and 1979. Subplots 4.1 × 6.1 m were situated in the same locations as those monitored in 1977. Soil samples were again taken and ID determined in the subplots. Disease ratings were made from late June until mid-September.

Approximately 350 plants were observed weekly in each of the six continuous cotton plots from the time of first square formation until mid-September. Newly diseased plants were tagged weekly to identify when foliar symptoms (FS) first appeared. At 1- to 3-wk intervals from emergence until late-September, five healthy-appearing plants (NoFS) were pulled from each plot. Also, five plants from groups of plants tagged as having early-, middle-, and late-season foliar symptom appearance times were pulled at 1- to

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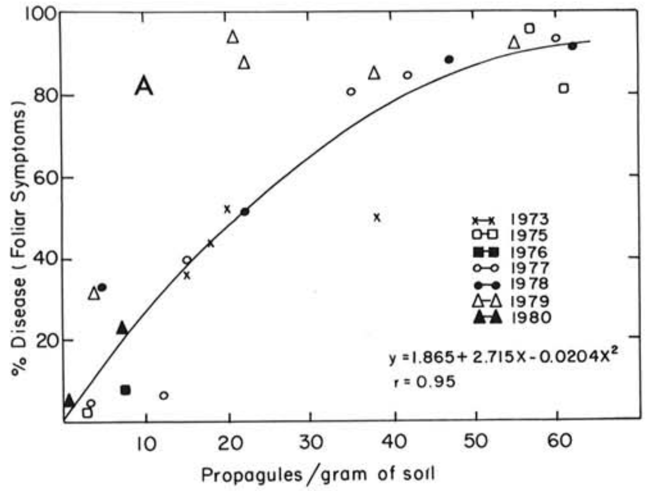

Fig. 1. Relationships between inoculum density of *Verticillium dahliae* in May and disease incidence (foliar symptoms) of Verticillium wilt in mid-September in a cotton field near Five Points, CA. Each data point represents an average inoculum density and disease incidence from six subplots that received the same soil treatment in previous years.

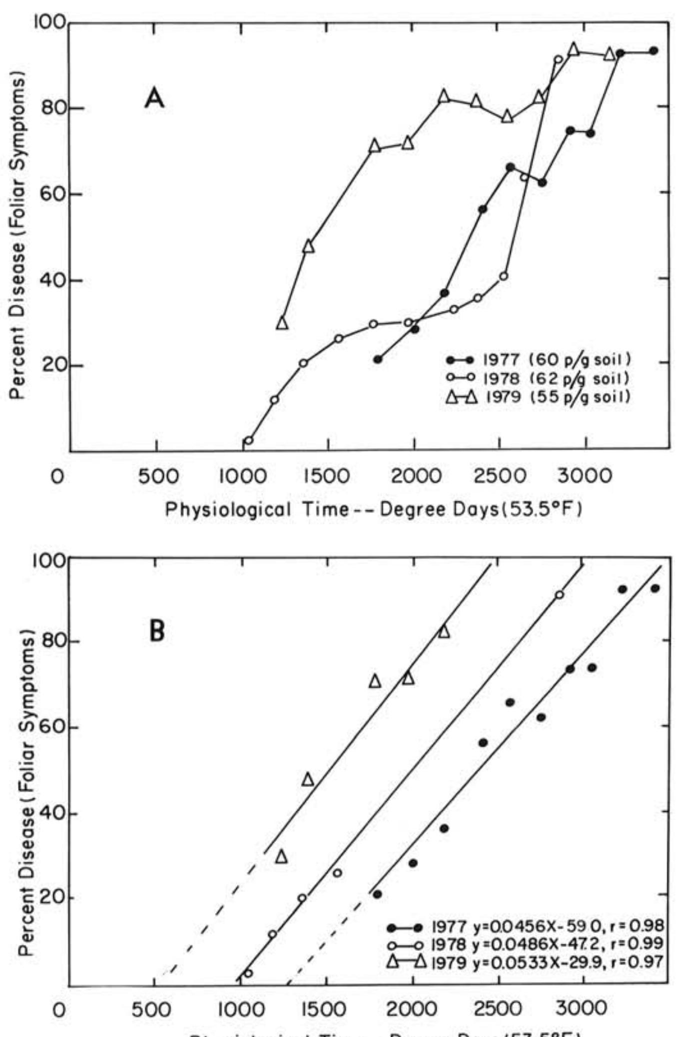

Fig. 2. Verticillium wilt of cotton in California. **A,** Percent disease incidence (foliar symptoms) as a function of physiological time. **B,** Percent disease before or after periods of high air temperatures (above 38 C) plotted against physiological time. Note that when disease ratings taken during periods of high air temperatures are removed, the relationship between % disease and physiological time becomes arithmetically linear. P/g stands for initial propagules of *Verticillium dahliae* per gram of soil.

3-wk intervals from the time of disease appearance until late September. All collected plants were cut at the cotyledonary node and observed for vascular discoloration or browning. Because all plants with foliar symptoms also showed vascular browning (VB), it was possible to calculate the total percentage of the population of plants with VB. With the percentage of VB known in plants without foliar symptoms (NoFS), and the percentage of plants with FS known, the total percentage of plants with VB was calculated as follows: Total % VB = FS + [(% NoFS) × (% VB in NoFS plants)]/100.

Field experiments, 1980. As part of a continuing study on the long-term effects of soil solarization, half of the 0.5-ha field used during 1977 was divided into six 10 × 45-m plots. These plots were arranged in a randomized complete block design with two treatments and three replications. Plots were covered with transparent 25-μm polyethylene plastic from 27 June to 2 August, 1979, or left fallow. These two treatments provided two sets of plots with different soil population densities of *V. dahliae*. All plots were planted in April with Acala SJ-2 cotton. Inoculum densities were determined in May 1980, and plants were examined weekly for foliar symptoms from early July until mid-September.

Determination of soil population densities of *V. dahliae*. During 1975–1980, soil samples were collected in May from each plot or subplot of the various treatments. Soil samples consisted of 10–12 cores each 2.5 × 30 cm. Cores were bulked for each plot, broken into small clumps and air-dried for 6–10 wk, and milled in a 5-L revolving jar mill for 20 min. The dry-soil plating technique of Butterfield et al (6) was used to spread five 100-mg samples of soil onto a selective sodium polypectate medium with an Anderson air sampler (Anderson Air Samplers, Atlanta, GA 30336). Microsclerotial colonies of *V. dahliae* were counted with the aid of a stereodissecting microscope after incubation at 20–24 C for 14 days. As few as two propagules per gram (p/g) of soil of *V. dahliae* could be detected with this technique. The soil population densities from 1972 to 1975 were determined by Butterfield et al (7) who sampled soil from the same field and used the same techniques to assay for *V. dahliae*.

Characterization of field isolates of *V. dahliae*. Approximately 100 cotton leaves with foliar symptoms of Verticillium wilt were collected at random several times during the 1975 and 1976 growing seasons. A portion of the petiole nearest the leaf base was excised, surface sterilized in 0.5% sodium hypochlorite for 2 min, and rinsed in sterile water. Individual petioles were ground by using a sterile mortar and pestle, mixed with 10 ml of sterile water, and 0.1-ml aliquots were plated onto Ohio Agar (16) supplemented with 50 μg of tetracycline-HCl per milliliter. Single colonies of *V. dahliae* were transferred to potato-dextrose agar (PDA) slants for storage. Isolates were transferred from stored culture to fresh PDA slants and after 7 days at room temperature (22–24 C) conidial masses were present from which conidial suspensions of 10^7 conidia per milliliter were prepared. Stems of three 6-wk-old plants of two cotton cultivars, Acala SJ-2 and 70-110, were punctured and inoculated each with three 25-μl droplets of the conidial suspension. Cultivar 70-110 was chosen for its high field susceptibility to Verticillium wilt. Inoculated plants were grown three plants per pot in 10.2-cm-diameter pots containing a mixture of sand and Yolo loam (1:1, v/v). Pots were placed in a glasshouse at temperatures between 22–24 C. Control treatments consisted of injections with distilled water or inoculations with isolates SS4 (nondefoliating), or T9 (defoliating) of *V. dahliae*. A total of 96 isolates were tested. After 6–7 wk, plant appearance within each pot was rated on a scale of 0–5 as follows: 0 = no visible symptoms of Verticillium wilt; 1 = mild chlorosis and necrosis; 2 = mild shriveling and moderate necrosis of leaves, with leaf remaining alive; 3 = rapid shriveling, severe necrosis, and death of leaf which remained attached to the plant; 4 = partial defoliation and stunting of plant; and 5 = plant stunting with rapid defoliation.

Physiological time. Maximum and minimum air temperatures were obtained from a weather station on the University of California West Side Field Station, located approximately 0.5 km from the field plots. Physiological time was determined as an accumulation of daily temperatures above 53.5 F (11.9 C) in units of Fahrenheit degree days (D°). Degree days were calculated by using a computer program that integrated the area under sine curves passing through the daily maximum and minimum air temperatures and above the cotton plants developmental threshold at 53.5 F (13). Degree days more adequately reflect the growth of cotton plants than Julian days and have been used successfully in predicting developmental times for cotton (13). Physiological time calculated in Fahrenheit degree days can be converted to centigrade degree days by multiplying by 0.555.

RESULTS

Population density and incidence of disease. The general relationship between ID in May near the time of planting and DI in mid-September is shown in Fig. 1. The curve was drawn from a curvelinear regression analysis of ID:DI over 7 yr; each data point represents an average of six subplots per year that had received a common soil treatment in previous years. Although each yearly set of data represents separate experiments, their presentation as a regression analysis of averaged data more clearly approximates the relationship between ID and DI. The ID:DI plot passes near the origin, and plateaus at about 40 p/g of soil. The population density required for 50% disease was approximately 19 p/g soil.

Disease incidence in mid-September often did not reach 100%. Disease ratings were not continued past mid-September because at this time cotton plants in the San Joaquin Valley often undergo senescence, which interferes with the recognition of foliar symptoms of Verticillium wilt.

Disease increase with time. Figure 2A shows disease progress curves for 3 yr as functions of physiological time and high ID (55–62 propagules of *V. dahliae* per gram of soil). Disease increased arithmetically with time for 1977 (slope value = 0.0456, $r = 0.98$) (Fig. 2B). In 1978, a midseason 4-wk period of daily air temperatures exceeding 38 C inhibited the progression of Verticillium wilt. Two to three weeks after the air temperatures decreased, there was a rapid increase in plants with foliar symptoms (Fig. 2A). When the slope value of the disease progression plot was calculated excluding the high-temperature period, a straight-line trend similar to 1977 was obtained (slope value = 0.0486, $r = 0.99$) (Fig. 2B). In 1979, a temperature inhibition of Verticillium wilt also occurred, this time towards the end of the growing season (Fig. 2A). Linear regression analysis based on disease ratings taken before the hot weather again showed a highly significant arithmetic relationship between disease and time (slope value = 0.0533, $r =$ 0.97) (Fig. 2B). Thus, the three disease progression curves all exhibited a straight-line increase in disease with time and showed similar slope values when adjusted for periods of high temperatures (Fig. 2B). The disease progress curve for 1975 from the same areas also showed a linear increase of disease with time (slope value = 0.0424, r = 0.95) for 57 p/g of soil (Butterfield and DeVay, *unpublished*).

When disease progress curves were plotted for levels of inoculum less than 40 p/g of soil, the slope values decreased as the ID decreased (Fig. 3). At ID less than 40 p/g of soil, all data points for a disease progress plot were used to calculate the line of best fit by regression analysis, regardless of air temperature conditions at the time of the data collection. It should be emphasized that during years of disease inhibition by high air-temperature, the use of all data points may underestimate the potential slope value which would occur at specific ID levels under ideal environmental conditions. The slope value of these disease progress curves and for 1979 (Fig. 2) are plotted against propagules per gram of soil for

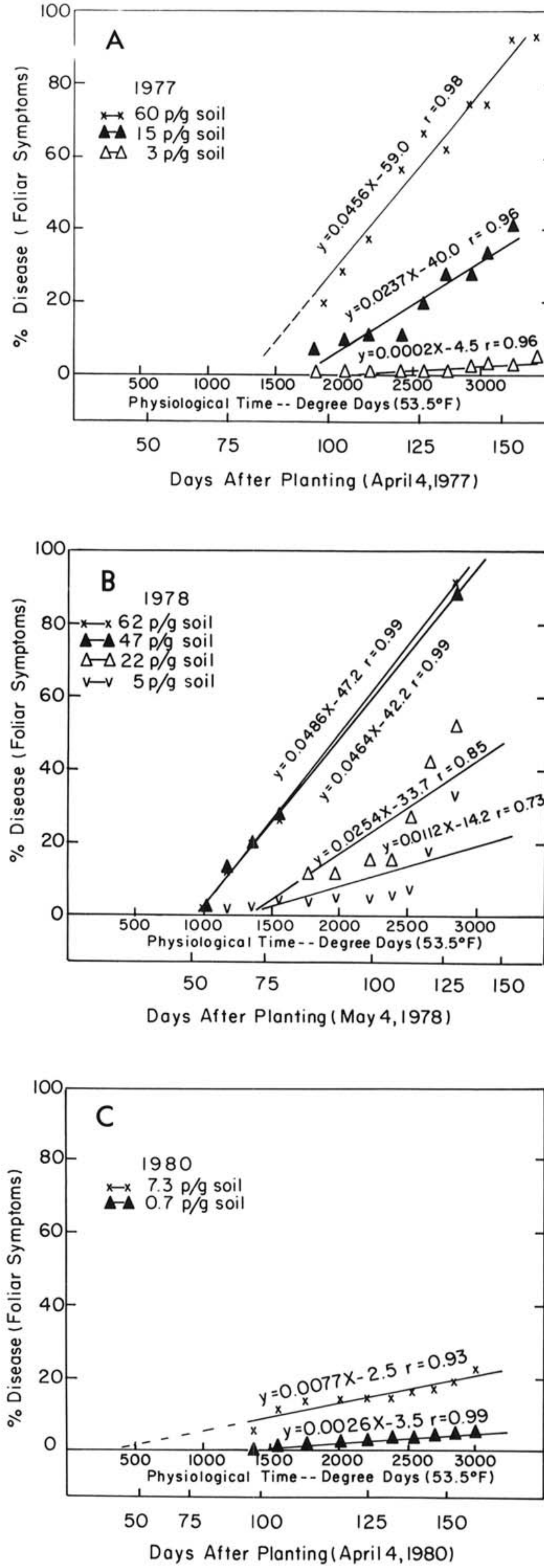

Fig. 3. The effect of initial inoculum density (p/g = propagules per gram) of *Verticillium dahliae* on the rate of appearance of foliar symptoms of Verticillium wilt in cotton in California. Disease appearance is plotted against physiological time (degree days) and chronological time from planting for: **A,** 1977; **B,** 1978; and **C,** 1980. Due to the inhibition of foliar symptom appearance by high air temperatures, the 1978 plots for inoculum densities greater than 40 p/g (propagules per gram) of soil only use disease readings taken before or after a 4-wk period of air temperatures with daily maxima generally >38 C.

May of each year in Fig. 4, and indicate the highly significant relationship between ID and the rate of foliar symptom appearance.

The weekly incidence of vascular browning and foliar symptoms during 1978 and 1979 is shown in Fig. 5. Both years had periods of high temperatures, which inhibited the development of foliar symptoms of Verticillium wilt. Air temperatures consistently greater than 38 C occurred from approximately day 74 to 99 (1,435–2,231 D°) during 1978 and from day 89 to 109 (1,584–2,182 D°) during 1979. Percentage of plants with vascular browning increased linearly with time throughout the season until almost all plants were affected. Resulting slope values for the increase of vascular browning over physiological time for 1978 were 0.0458 ($r = 0.94$) and 0.0366 for 1979 ($r = 0.99$). In 1979, only data points between 1,000 and 2,500 D° were used in the regression analysis because after that period of physiological time 100% of the sampled plants showed vascular browning. Foliar symptoms, however, always developed after the occurrence of vascular browning, and during periods of high temperatures the percentage difference between these two symptoms increased.

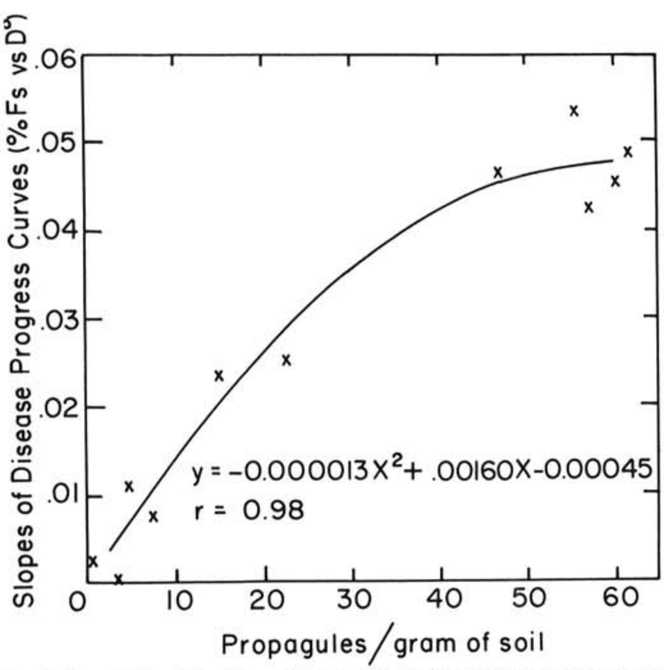

Fig. 4. The relationship of inoculum density of *Verticillium dahliae* to the slopes of disease progress curves (percent foliar symptoms vs degree days) for Verticillium wilt of cotton in California in 1975 and 1977–1980.

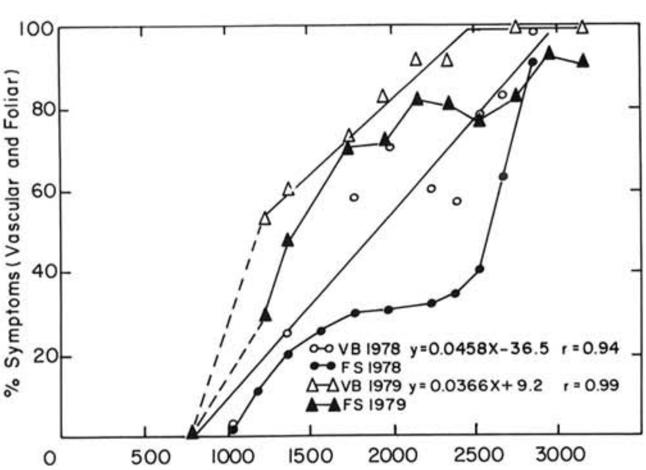

Fig. 5. Verticillium wilt of cotton in California. A comparison of vascular browning (VB) and incidence of foliar symptoms (FS) with physiological time. During 1978 and 1979, maximum air temperatures ⩾38 C occurred from 1435–2231 and 1584–2182 degree days, respectively.

Seasonal increase of inoculum. Soil inoculum densities of *V. dahliae* were monitored over a period of 4–7 yr in two sets of plots to determine changes in population densities of *V. dahliae* (Fig. 6). In the first treatment, soil was cropped continuously to Acala SJ-1 and SJ-2 cotton from 1972–1978 and ID increased by approximately 13 p/g of soil per year, until 1976 when populations began to level off. In the second treatment, where a single crop of paddy rice was grown during 1974 (7,19), *V. dahliae* reinfested the soil from a level of 3 p/g of soil at a rate of approximately 15 p/g of soil per year from 1975–1978. Soil inoculum densities for the years before 1976 were obtained from Butterfield et al (7).

Characterization of isolates of *V. dahliae*. Reactions of cultivars Acala SJ-2 and 70-110 to 96 leaf isolates of *V. dahliae* were tested. Severe defoliating isolates of *V. dahliae* similar to T9 were not detected in the field studied, although approximately 9% of the isolates were classified as defoliating types due to a partial defoliation of inoculated plants. Sixty-five to 77% of the isolates were intermediate types and gave a rating between 2.0 to 4.0 in Acala SJ-2 and 70-110, respectively, compared to SS4 and T9, which gave ratings of 0.9 to 1.5 and 4.7 to 4.9, respectively. The remaining isolates were nondefoliating.

DISCUSSION

This study was concerned mainly with the relationship between inoculum density and the progressive development of Verticillium wilt. Earlier literature on the relationship between Verticillium wilt and ID has been reviewed by Erwin (10).

The incidence of infection, as measured by vascular discoloration at the time of harvest, is closely related to ID at the time of planting (2,5). However, disease incidence as indicated by the presence of leaf symptoms was variable and did not always reflect ID when many fields were compared (5,9). Cropping history, fertilization practices, cultivars of cotton, row spacing, fungal pathotypes present in one field versus another, and daily temperatures have major effects on foliar symptom development. The present study was done at a single location to avoid some of these variables, especially wide differences in pathotypes of *V. dahliae*.

The view that in a single location a predictable relationship may exist between ID and foliar disease was confirmed over a period of 7 yr in the fields that we studied. However, while disease incidence and ID increased, the ratio of disease to ID decreased (Fig. 1). These results agree with the predictions of Vanderplank (26) for simple interest diseases in which inoculum is competing for infection sites.

In any model of plant disease, it is important to determine the

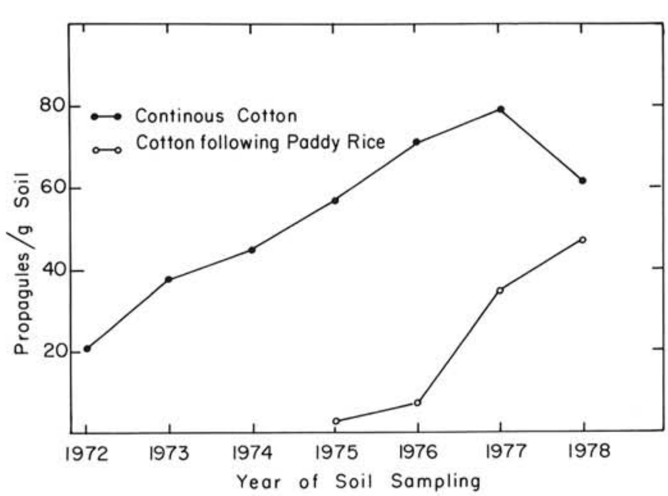

Fig. 6. Annual increase in inoculum densities of *Verticillium dahliae* in plots cropped with cotton from 1972–1978 and in plots cropped with cotton from 1975–1978 following a single crop of paddy rice.

rate of disease progression in plant populations throughout the season. Graphical plots consistently indicated highly significant straight-line relationships between percent disease increase and time for various levels of inoculum. When inoculum densities were greater than 40 p/g of soil, the disease progress curves had slope values (% disease vs D°) that varied between 1.15 and 1.42. At levels of inoculum less than 40 p/g of soil, the slope values of the disease progress curves decreased as the level of inoculum decreased (Figs. 3 and 4). Similar disease progress curves, which appear to fit straight lines, have been reported by Ashworth and Huisman (1) for high levels of inoculum with several cultivars of Acala cotton.

The relationships between ID and DI is such that the incidence of Verticillium wilt throughout the season can be predicted at this particular field site if the ID is known, the relative percentages of pathotypes remain constant and environmental factors such as temperature do not inhibit disease development. The relative percentages of pathotypes appear to have remained unchanged from 1975–1978, as both Butterfield (*unpublished*) in 1975 and Friebertshauser (11) during 1977–1978, characterized leaf isolates of *V. dahliae* from the same field site and found mainly nondefoliating and intermediate pathotypes. Because the development of foliar symptoms is directly proportional with time, the rate of disease development early in the season can also be used to predict the probable incidence of disease later in the season, providing air temperatures inhibitory to disease development are of short duration.

At higher ID, the line of best fit for the disease progress curves usually intersected the time axis between 30 to 80 Julian days or 500 to 1,300 degree days after planting. Once the disease increase began, it continued at a constant rate unless inhibited by high air temperatures. Therefore, it appears that some factor was conducive for disease development and that once this occurred, the percentage of plants with foliar symptoms increased arithmetically with time. It is probable that the disease-conducive factor is related to the soil water status and subsequent root growth. The first irrigation in the experimental plots, given in mid-to-late June, often coincided with rapid plant growth and development. The root system also increased rapidly at this time and provided increased root surface for inoculum contact. In some studies, the number and duration of irrigations affected the incidence of Veritcillium wilt in cotton (3).

Differences between vascular browning and foliar symptoms may have been induced by the environment. The percentages of plants with foliar symptoms were always less than the percentages of plants with vascular browning. This difference increased to an even greater extent during periods of high temperatures. These results suggest that plants were infected at a constant rate throughout the growing season and that the rate was not altered by high air temperature. Disease development, however, resulting in plant stunting, foliar symptoms, and loss in yield was greatly influenced by air temperatures, which at times completely inhibited disease expression until cooler weather occurred.

The inhibition of disease development by heat has been reported both in field and greenhouse studies (3,12). Conidia of *V. dahliae* generally do not germinate at temperatures above 30 to 33 C, mycelial growth ceases at temperatures above 33 C, and temperatures above 36 C can kill all fungal structures if maintained for sufficient periods of time (21,25). This heat inhibition can be extremely important for plant yield, as yield loss is directly related to the time of foliar symptom appearance (20).

The increase of inoculum averaged 13–15 p/g of soil per year when almost all plants were infected and showing vascular browning. This increment in inoculum production in itself was enough to cause 100% infection at harvest (5) and 40% disease in mid-September. Thus, a field with 5–10% disease can increase to 80–90% disease after two to three successive cotton crops. Huisman and Ashworth (14) also have reported similar rapid increases in ID following several crops of cotton.

The relationship between ID in soil and the frequency of root infection that results in foliar symptoms and stunting of plants is unclear. Fields often contain heterogeneous populations of *V. dahliae* that vary greatly in virulence. In greenhouse experiments, Schnathorst and Mathre (24) showed that isolates varying in virulence to cotton also varied in the amount of inoculum required to produce a certain incidence of disease. The defoliating isolate (T-1) caused more disease at a lower ID than did a nondefoliating isolate (SS4) at much higher inoculum densities. Because the present study was based on a field containing mainly nondefoliating and intermediate pathotypes of *V. dahliae*, the ID:DI ratios and corresponding slope values of disease progress curves are probably less than those for fields containing inoculum of the defoliating pathotype. Compounding this relationship even further, nondefoliating strains of *V. dahliae* and other *Verticillium* species can exhibit the phenomena of cross-protection (17,23). Inoculum density can be determined easily by several methods; however, simple techniques to determine virulence need to be developed (6,15). Virulence has been correlated with the ability to detoxify the alkaloid compound, sanguinarine; however, only isolates of *V. dahliae* of extremes in virulence can usually be identified (18).

The results of this study indicate that within an individual field, the incidence of Verticillium wilt resulting in plant stunting, foliar symptoms, and loss of yield, can be predicted throughout a growing season based on the ID at the time of planting. With the development of rapid techniques to assay inoculum density and determine inoculum virulence, ID:ID relationships can probably be extended to many fields of diverse pathotypes and populations of *V. dahliae*.

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